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The importance of cenotes in conserving bat assemblages in the Yucatan, Mexico

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ABSTRACT

In the Yucatan, cenotes or water sinkholes formed by the dissolution of limestone and surrounded with a characteristic dense layer of heterogeneous vegetation, are the main sources of water for plant and animal assemblages. We investigated their importance to bats by comparing the assemblage structure and diversity between tropical forest and pastureland, with and without cenotes. We set ground level mist nets, sub-canopy nets and harp traps for 96 nights and caught 2819 bats of 26 species and six families. Forest had a greater bat species diversity and abundance than pastureland, as well as rare and threatened species. In forest, sites with and without cenotes had a similar bat assemblage structure and diversity, whereas in pastureland there was a greater species diversity and abundance and number of rare and threatened species at cenotes than sites without cenotes. *Chrotopterus auritus* and *Miconycteris schmidtorum*, both threatened in Mexico, and *Eptesicus furinalis*, were exclusively captured at cenotes. We suggest that it may be the vegetation around cenotes rather than the water bodies *per se* that attracts many bat species in pastureland. Cenotes are threatened by nitrate contamination from untreated domestic and animal waste and fertilizers and the removal of vegetation to allow livestock access to water. In Yucatan's agricultural landscapes, protection of cenotes and their characteristic vegetation is key not only for bat conservation but also because they represent potential seed sources for the regeneration of the lowland forest, in which bats play key roles as pollinators and seed dispersers.

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1. Introduction

The Yucatan Peninsula is a predominantly flat limestone region in the southeast of Mexico, divided into the states of Campeche, Quintana Roo and Yucatan. The vegetation over much of the Peninsula has been modified since Mayan times (1000 BC), but the extent and intensity of such change increased significantly after the arrival of Spanish colonizers and particularly in the last century. These changes in the vegetation are more evident in the north of the Peninsula,

particularly in Yucatan where crops and man-made pasturelands are abundant (INEGI, 2006). Quintana Roo, in contrast, has large areas of disturbed forest that have been left to regenerate for more than 50 years (Schultz, 2005).

A remarkable feature of the Peninsula, especially in the north, is the presence of cenotes. Cenotes (from the Mayan word *dzonot*) are water-filled sinkholes formed by the dissolution of limestone by carbonic acid and are the only visible signs of the distinctive underground aquatic system of the Yucatan Peninsula (Cervantes-Martínez et al., 2002). Cenotes

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are numerous and represent the main source of fresh water for humans and wildlife. Ecologically they are considered as islands of aquatic life and they have distinctive vegetation due to the presence of tall evergreen trees such as *Ficus* spp. (Flores and Espejel, 1994). The majority of studies investigating the association of animal life with cenotes have focussed on fresh water invertebrate communities and fish assemblages, whereas other animal groups such as birds and bats have received little attention (Schmitter-Soto et al., 2002).

Bats represent the second largest order of mammals in terms of number of species, with over eleven hundred species described (Simmons, 2005) and exhibit the greatest diversity of feeding habits (Kalko et al., 1996). The ecology of neotropical bats has been extensively studied and the ecological role of some bat species as seed dispersers, pollinators and predators of insects and vertebrates is well known (e.g. Heithaus et al., 1975; Simmons and Voss, 1998; Medellín and Gaona, 1999). The high diversity of bats depends on a complex partitioning of resources such as food and roosts (Findley, 1993; Aguirre et al., 2003).

Water bodies, particularly those with calm surfaces, represent important foraging sites for insectivorous bats (Ciechanowski, 2002; Russ and Montgomery, 2002) as the air above them is usually rich in insects (Rydell et al., 1999). On the other hand, bat species with different feeding requirements such as most frugivore, nectarivore and gleaning insectivore species depend on mature heterogeneous vegetation to sustain their populations (Cosson et al., 1999).

The calm waters of cenotes and the typical forest surrounding them have the potential to attract and maintain

a high diversity of bat species, particularly in the Yucatan's largely deforested agricultural landscape. Sosa-Escalante (1997) found a high diversity of terrestrial mammals in deciduous forests in Yucatan and suggested that the presence of cenotes is the main factor responsible. More recently, analysis of echolocation calls of insectivorous bats in Yucatan indicated a preference for cenotes as foraging sites by some species (Rydell et al., 2002). However until now there remains a paucity of information regarding the importance of cenotes in structuring bat assemblages. In this study we address this question in two contrasting habitats: pastureland and forest, in order to investigate the structure of the bat fauna in sites with and without cenotes. We test the hypothesis that higher bat diversity is associated with forested habitats and cenotes, by evaluating species diversity, composition and abundance, both spatially and temporally. Our overall aim is to provide a relatively complete inventory of bats for the north of the Yucatan Peninsula and to investigate the importance of cenotes in structuring bat assemblages to gather baseline information to guide conservation efforts.

2. Methods

2.1. Study area

The bat assemblage was sampled at eight locations: two cenotes in pastureland, two cenotes in forest, and two sites in each vegetation type without cenotes (and an absence of water bodies within 4 km) (Fig. 1).

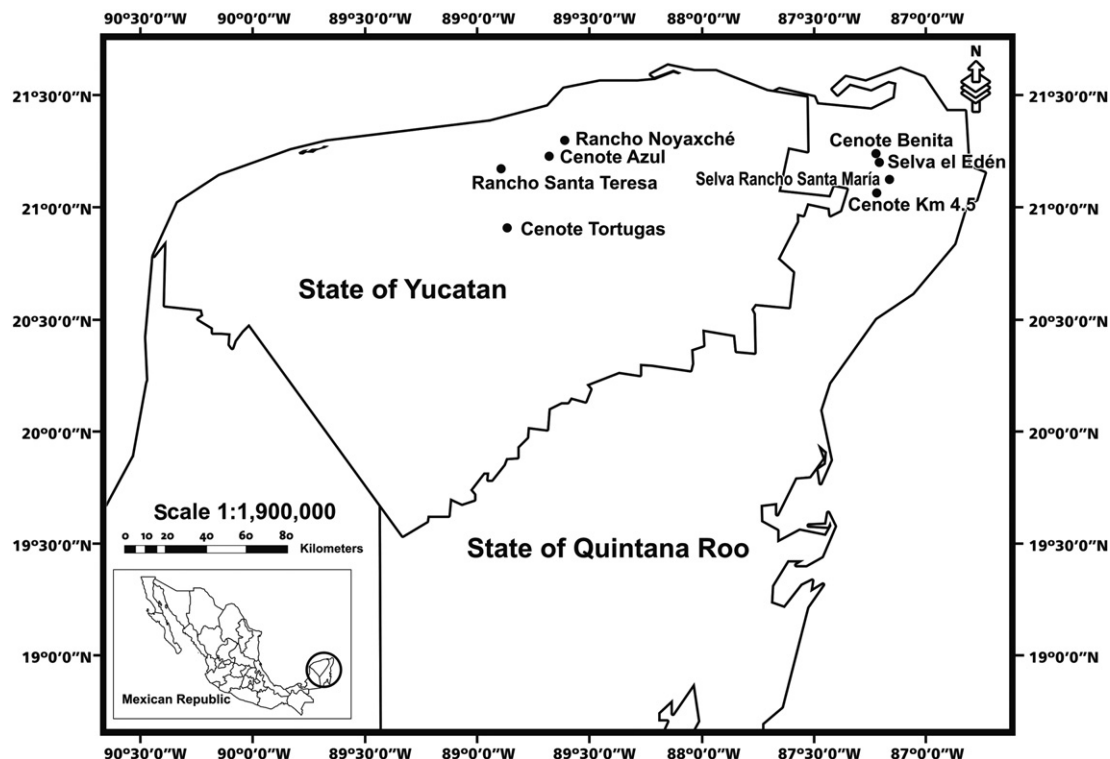


Fig. 1 – Map of the Yucatan Peninsula, Mexico. Sampling sites in pastureland are located in the state of Yucatan. Forested sites are located in the state of Quintana Roo.

2.2. Pastureland sites

Pastureland sites were located in the cattle zone east of Merida, the capital of the state of Yucatan. This zone was originally comprised of semi-deciduous forest of medium-stature (Flores and Espejel, 1994), but has been modified by Mayan civilizations and recently for the intensive cultivation of henequen (agave: *Agave fourcroydes*) which is used to produce rope and other fibre products (González-Iturbe et al., 2002; Gómez-Pompa, 2003). Currently this area is characterised by extensive cattle ranching with plantations of *Pennisetum purpureum*, *P. ciliare*, *Panicum maximum* and other grasses, stands of secondary forest with different stages of succession and some scattered trees such as *Ficus* spp., *Ceiba pentandra*, *Terminalia catappa* and *Brosimum alicastrum*. Landowners allow some of these trees to remain as they provide shade and food for the cattle. Annual rainfall is 900–1037 mm and average temperatures range from 25.9 to 26.4 °C (Barber et al., 2001). Sites were about 7–13 m above sea level.

Pastureland without cenotes: Sampling sites were Rancho Santa Teresa (N 21°10', W 88°53') and Rancho Noyaxche (N 21°17', W 88°36').

Cenotes in pastureland: Cenote Azul (N 21°13', W 88°40') and cenote Tortugas (N 20°54', W 88°51') were about 50–65 m in diameter with a surrounding vegetation belt 30–50 m wide. Dominant tree species were *Ficus* spp., *Acacia pennatula*, *Caesalpinia gaumeri*, *Lysiloma latisiliquum*, *Metopium brownie*, *Manilkara zapota*, *Vitex gaumeri*, *Bursera simaruba* and *Gymnopodium floribundum*. Cenotes and their vegetation belt were surrounded by pastureland landscape.

2.3. Forest sites

Forested sites sampled for bats were located in the north of the state of Quintana Roo within protected private reserves. The forest contains evidence of a variety of both human and natural disturbances. Human disturbances include Pre-classic Maya settlements (900–300 BC), timber extraction (late nineteenth century), and chicle (chewing gum) extraction (dates unknown) while hurricanes are the main natural disturbances (Schultz, 2003). The predominant vegetation type was mature semideciduous forest of medium-stature, more than 50 years old and characterized by trees of 15–20 m average height. Dominant tree species were: *Manilkara zapota*, *M. brownie*, *L. latisiliquum*, *Thrinax radiata*, *B. simaruba*, and occasional large individuals of *B. alicastrum*, *Ficus pertusa* and *Acacia dolichostachya* (Schultz, 2003). Annual mean temperature is 23.7 °C and rainfall is 1124 mm (Barber et al., 2001). Elevation was about 5–10 m above sea level.

Forest without cenotes: Sampling sites were Selva Rancho Santa María (N 21°06', W 87°10') and Selva El Eden (N 21°12', W 87°12').

Cenotes in forest: Cenote Benita (N 21°13', W 87°12') and Cenote Km 4.5 (N 21°04', W 87°12') were 30–70 m in diameter. Dominant trees species were *M. zapota*, *Ficus* spp., *M. brownie*, *V. gaumeri* and *Haematoxylon campechianum*.

2.4. Capture methods

Fieldwork was conducted in 2003, 2004 and 2005. Each of the eight locations was visited for three nights during both the

dry and wet seasons for a two-year period for total of 96 nights of sampling. We avoided sampling on consecutive nights at the same location to prevent bats from learning the position of the nets which could result in reduced capture rates (Kunz and Kurta, 1988). No fieldwork was scheduled around the full moon because of its inhibitory effect on bat activity (Morrison, 1978; Elangovan and Marimuthu, 2001) and trapping was suspended during heavy rain.

Each night five 12 × 2.6 m mist nets of 36 mm mesh size, two-ply, and with four shelves (AFO Mist Nets, Manomet, Inc.) were erected at ground level (0–3 m). A 12 × 3 m mist net modified to become an 8 × 3 m sub-canopy mist net (Avinet Inc., Dryden, NY) was set following the method initially described by Munn (1991) and modified by Clarke et al. (2005b). A four-frame harp trap (Francis, 1989) with a catching surface of 1.42 m² was set in trails.

Nets and the harp trap were set at sunset, left open for an average of 7 h and monitored every 30 min. We estimated capture rate for each catching method by dividing the number of bats captured by the number of mist net hours (bats/mnh) or harp trap hours (bats/hth). Mist net hours were calculated as the length of all nets set multiplied by the number of hours they were left open (Medellín, 1993). We standardized catching methods to achieve an equal sampling effort among sites.

Bats were identified to species level with field keys (Medellín et al., 1997; Reid, 1997), measured, either marked with temporary non-toxic paint or with aluminium numbered forearm rings and then released at the capture site within 3 h of capture. Bat taxonomy follows Simmons (2005). Bats were categorized as juveniles or adults by examining the extent of phalangeal ossification (Anthony, 1988). Reproductive assessment followed Racey (1988). Recapture rate was low (0.17%, $n = 5$) and recaptures were not considered in analyses. We defined locally rare species as those species contributing <0.5% of the total captures.

Finally, voucher specimens were collected for species whose identity required confirmation and deposited at the Regional Zoological Museum (COZORE) at the Autonomous University of Yucatan (UADY) in Mexico.

2.5. Statistical analyses

A species accumulation curve was plotted to assess completeness of sampling effort at each site. We estimated the true species richness (S_{max}) with the non-parametric Chao's quantitative estimator (Chao, 1984). We calculated inventory completeness as $S_{obs}/S_{max} \times 100$.

To compare bat abundance among sites we constructed rank/abundance plots and statistically compared differences in species abundance distributions with a Kolmogorov–Smirnov two-test (Magurran, 2004). We used Wilcoxon's signed rank test (T) to investigate seasonal patterns in bat species abundance. Nightly capture rates were compared with a one-way analysis of variance (ANOVA) (F), using Fisher's LSD test if the ANOVA result was significant (Dytham, 2005).

We determined alpha diversity using Simpson's index (D) (Simpson, 1949), a robust measure that considers the variance of the species abundance distribution. Simpson's index values given are the reciprocal value ($1/D$). Bat diversity was compared between sites and seasons using randomization

tests with 10,000 partitions (Solow, 1993). We calculated dominance with the Berger–Parker index (d) that expresses the proportional abundance of the most abundant species: $d = N_{\max}/N$ (Berger and Parker, 1970).

We assigned bat species into the following broad trophic guilds according to diet and foraging behavior (Simmons and Voss, 1998): (1) aerial insectivores (all non-phylostomids), (2) frugivores (carollines and stenodermatines), (3) gleaning animalivores (all phyllostomines), (4) nectarivores (glossophagines), and (5) sanguivores (desmodontines). Number of species in each guild were compared with a Chi square test (χ^2), considering the forest site as the model for expected values.

Finally, we compared species composition between sites with the Bray–Curtis similarity index, which takes account of the relative abundance of species (Magurran, 2004). Values of similarity are expressed in percentages. Data was analyzed with Species Prediction and Diversity Estimation (Chao and Shen, 2003–2005), Species Diversity and Richness version 2.6 (Pisces Conservation Ltd., Lymington, Hants, UK) and Mini-tab14 (Minitab Inc., State College, PA, USA).

3. Results

3.1. Capture success

A total 2819 bats of 26 species and six families was captured (Table 1). Capture rates with ground nets and harp traps were significantly lower in pastureland without cenotes than other sites (ground nets: $F = 8.6$, $df = 3$, $p < 0.01$; harp trap: $F = 4.6$, $df = 3$, $p < 0.01$; Fisher's LDS test) but were similar for the sub-canopy nets (Table 2). Sub-canopy nets were significantly more effective at capturing bats in pastureland without cenotes than ground nets ($F = 6.7$, $df = 1$, $p = 0.01$). Harp traps were the least effective catching method in terms of number of individuals and species captured. We captured 16 species with more than one method, but five species were exclusively recorded in the ground mist nets, three species in the sub-canopy nets and two species in the harp traps (Table 1).

3.2. Species diversity and relative abundance

The species accumulation curves (Fig. 2) suggest that our sampling effort provided a good representation of most of the species that could be captured using our methods. Twenty-one species (80% of species captured) were recorded in the first 31 nights of sampling, with only five rare species recorded in the following 65 nights. The forest had the highest number of species (20) and the pastureland without cenotes had the least (14). The average number of species captured per night was 5.33, 5.25, 4.54 and 3.08 in forest, cenotes in pastureland, and pastureland, respectively.

We captured 26 species in the north of the Yucatan Peninsula, but we estimate true species richness (S_{\max}) to be 34 species; our overall inventory completeness was therefore 76%. It ranged from 58% to 80% in the four sites (Table 1).

The Phyllostomidae was the best represented family with 17 species and phyllostomid bats accounted for 95% of the captures in our study, whereas the Emballonuridae, Natalidae

and Molossidae were each represented by only one species and relatively few captures. *Artibeus jamaicensis* was the most abundant species in all sites with 61–65% of captures. However, the second most abundant species differed between sites. It was the common vampire bat, *Desmodus rotundus*, in cenotes in pastureland, *Glossophaga soricina* in pastureland without cenotes, *Artibeus phaeotis* in cenotes in forest and *Artibeus lituratus* in forest. Fifteen species in the assemblage (46%) can be considered as rare with four species being represented by a single individual.

Capture rates among habitats differed significantly ($F = 7.5$, $df = 3$, $p < 0.01$). More bats were captured in habitats with cenotes than the same habitats without cenotes. This was particularly true for pastureland. The rank-abundance distributions were not significantly different between sites with and without cenotes (Fig. 3), (Kolmogorov–Smirnov two sample test cenote in pastureland vs. pastureland maximum difference: 0.088, $p > 0.50$; cenotes in forest vs. forest maximum difference: 0.034, $p > 0.50$). At most sites, bats were significantly less abundant during the dry season, except at cenotes in forest ($T = 74$, $N = 17$, $p = 0.754$).

The most diverse sites were the cenotes in pastureland ($1/D = 2.43$), followed by the cenotes in the forest, and then forest and pastureland without cenotes, though differences in diversity were not statically significant (Randomization test, $p = 0.05$). Pastureland was more dominated by a single species, *A. jamaicensis*, than the other sites (Table 1).

3.3. Guild composition and abundance

Overall, the aerial insectivore guild was the most speciose with nine species (35% of those in the assemblage) but at each site this guild was represented by few captures. Frugivores dominated in terms of number of species and individuals captured in each site, followed by aerial insectivores (Table 3). There were no significant differences in the number of species in each guild (all comparisons $\chi^2 < 7.8$, $df = 3$, $p > 0.05$). However, considerably fewer gleaning animalivores (species and individuals) were recorded in pastureland without cenotes compared to the other sites (Table 3). All sites were similar in the number of guilds present, the only exception being that sanguivores were not recorded in cenotes in the forest. The abundance of bats in each guild differed between forest without cenotes and all other habitats (cenfor: $\chi^2 = 16.1$, $df = 4$, $p = 0.05$; past: $\chi^2 = 533.6$, $df = 4$, $p < 0.001$; cenpast: $\chi^2 = 527.5$, $df = 4$, $p < 0.001$) (Table 3).

The greatest similarity in species composition was between the forest with cenotes and forest without cenotes (93%), then between pastureland with and without cenotes (63%). The least similar sites were the pastureland without cenotes and forest with cenotes (34%).

4. Discussion

4.1. Bat assemblage organisation and diversity

The Yucatan Peninsula bat assemblage has around 62 widely distributed species (Arita, 1993; MacSwiney et al., 2003), with a greater species richness in the south, probably as a result of

Table 1 – Number of bats of each species caught and diversity measures of the bat assemblage of the north of the Yucatan Peninsula

Taxon	Pastureland		Forest	
	Cenotes	No cenotes	Cenotes	No cenotes
EMBALLONURIDAE				
<i>Saccopteryx bilineata</i> ^a				2
PHYLLOSTOMIDAE				
Desmodontinae				
<i>Desmodus rotundus</i>	41	6		4
<i>Diphylla ecaudata</i> ^b				1
Glossophaginae				
<i>Glossophaga soricina</i>	19	39	16	30
Phyllostominae				
<i>Chrotopterus auritus</i> ^a	5			
<i>Lamproncycteris brachyotis</i> ^a			2	1
<i>Lonchorhina aurita</i>			13	10
<i>Micronycteris microtis</i>	3	5	6	
<i>Micronycteris schmidtorum</i> ^c	1			
<i>Mimon cozumelae</i> ^c	4		3	5
Carollinae				
<i>Carollia sowelli</i>			69	86
<i>Carollia perspicillata</i> ^c		1	1	1
Stenodermatinae				
<i>Sturnira lilium</i>	40	20		1
<i>Artibeus jamaicensis</i>	323	188	636	627
<i>Artibeus lituratus</i>	20	8	111	88
<i>Artibeus phaeotis</i>	21	4	125	80
<i>Centurio senex</i> ^a	1		1	3
<i>Chiroderma villosum</i> ^c	4	3	3	3
MORMOOPIDAE				
<i>Pteronotus parnellii</i>	28	2	30	31
<i>Pteronotus davyi</i> ^c	4			1
NATALIDAE				
<i>Natalus stramineus</i> ^c	1	4	2	2
MOLOSSIDAE				
<i>Molossus rufus</i> ^b		6		
VESPERTILIONIDAE				
<i>Eptesicus furinalis</i> ^a			1	
<i>Lasiurus ega</i> ^b		1		
<i>Rhogeessa aeneus</i> ^a	1	1	1	
<i>Myotis keaysi</i>	1		12	4
Diversity	CENPAST	PAST	CENFOR	FOR
Number of species (S_{obs})	17	14	17	20
True species richness (S_{max})	29.5	18.5	21	26.2
Simpson's diversity index (1/D)	2.43	2.19	2.42	2.33
Berger Parker's dominance index (d)	0.62	0.65	0.61	0.63
Number of locally rare species	8	6	8	9
Number of threatened species	3	0	3	3
CENPAST, cenotes in pastureland; PAST, pastureland; CENFOR, cenotes in forest; FOR, forest. S_{max} was calculated with Chao's quantitative index.				
* Rare species (contributing <0.5% of the total captures). Exclusively captured in: a ground level mist nets, b sub-canopy mist net, and c harp trap.				

increased forest cover, rainfall, humidity and temperature (Sosa-Escalante, 1997). Forty-four species have been recorded in the north of the Peninsula (e.g. Jones et al., 1973; Fenton et al., 1992; Hernández et al., 1996; MacSwiney, 2000) although Arita (1997) considers some of these records as misidentifications (e.g. *Myotis nigricans*, *Rhynchonycteris naso*) or doubted their presence (e.g. *Macrotus waterhousii* and *Corynorhinus [Plecotus]*

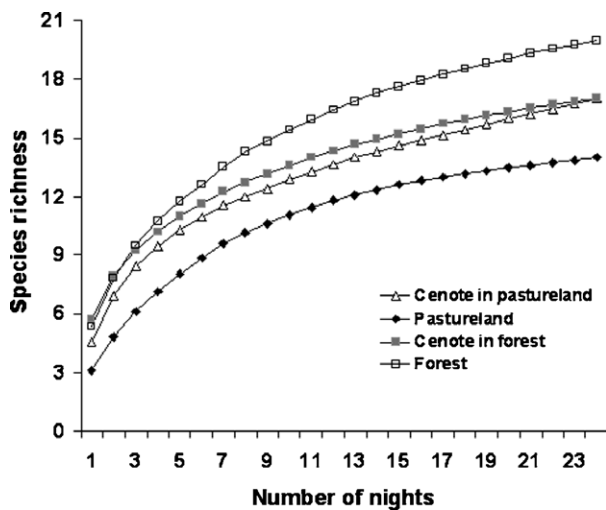
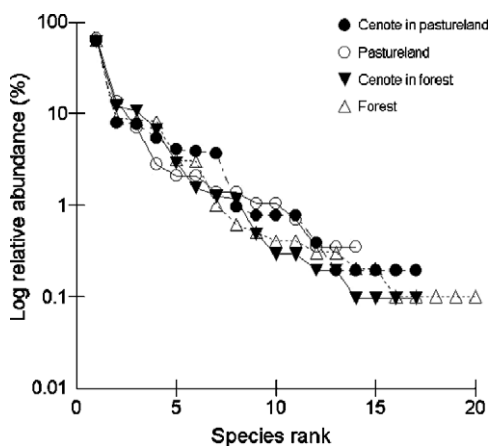
mexicanus). Additionally other species have been renamed (e.g. *Artibeus intermedius*, *Rhogeessa tumida*) (Audet et al., 1993; Simmons, 2005), so the current number of bat species recorded in the north of the Peninsula is likely to be 37. We recorded 26 species, more than in other bat community study, and thus provide the most complete and accurate representation of the bat assemblage of the northern Yucatan Peninsula to date.

Table 2 – Sampling effort of the catching methods per habitat

Habitat	Ground mist-net				Sub-canopy mist net				Harp trap			
	n	S	mnh ^a	Bats/mnh	n	S	mnh	Bats/mnh	n	S	hth	Bats/hth
CENPAST	437	13	239,760	0.0018	56	5	32,640	0.0017	23	8	159	0.14
PAST	158	9	241,920	0.0006	120	9	31,680	0.0036	8	3	164	0.04
CENFOR	873	16	240,048	0.0036	113	9	31,776	0.0035	45	9	161	0.27
FOR	859	15	246,240	0.0034	88	10	32,448	0.0027	39	9	163	0.23
Total	2327	21			377	16			115	13		

n, number of bats captured; S, number of species; mnh, mist-net hour; hth, harp-trap hour; CENPAST, cenotes in pastureland; PAST, pastureland; CENFOR, cenotes in forest; FOR, forest.

a mnh is the product of length of all nets in meters multiplied by the number of hours net were set.

**Fig. 2 – Bat species accumulation curve at all sites.****Fig. 3 – Rank-abundance plot for the sites sampled in the Yucatan Peninsula, Mexico.**

The Jamaican fruit-eating bat, *Artibeus jamaicensis*, a widespread species that often dominates neotropical assemblages over a wide range of habitats (Handley et al., 1991; Rodríguez-Durán and Vázquez, 2001) was the most abundant bat in all habitats. The second most abundant bat species varied according to habitat type. Large populations of the common vampire bat, *Desmodus rotundus*, indicate anthropogenically

disturbed habitats (Medellín, 1993) and this species was abundant at all our pastureland sites where livestock was plentiful. *D. rotundus* was especially numerous at cenotes in pastureland (8% of total captures) and was the second most abundant bat. This finding may be attributable to vampire bats being attracted to the trees surrounding the cenotes and approaching livestock by crawling along the underside of branches (Reid, 1997) or using the vegetation as ‘digesting places’ after feeding (Greenhall et al., 1983). Despite the abundance of *D. rotundus* in the cattle zone, local ranchers believed that this species does not pose an economic threat because of the effectiveness of ongoing government vampire control programmes. Clearly it is important that these campaigns are closely supervised to ensure that they exclusively target vampire bats and not other bat species.

The second most abundant bat species in pastureland without cenotes was *Glossophaga soricina*, a species that feeds mainly on nectar and pollen, but also consumes other floral parts and insects when nectar and pollen are scarce (Lemke, 1984). In pastureland without cenotes this species was frequently captured while feeding on the fruits of isolated *Ficus* spp. The feeding plasticity of this species contributes to its successful distribution across a broad type of habitats and its ubiquitous presence in other neotropical bat assemblages (Fenton et al., 2001). In contrast to pastureland, large *Artibeus* spp. were common in forest with *A. phaeotis* and *A. lituratus* being the second most abundant species in forest with and without cenotes, respectively. These frugivores forage in the forest sub-canopy and their abundance is associated with the availability of fruiting *Sapotacea* spp., *Brosimum*, *Ficus* and *Manilkara* (Schulze et al., 2000), all of which were abundant in our forested sites.

Fifteen species, 57% of those caught in our study, are considered rare. The present study supports the findings of Arita and Vargas (1995) that *Carollia perspicillata*, an abundant species in other areas, has small populations in the Yucatan. Specialization in microhabitat (*Micronycteris schmidtorum*, *Lampronnycteris brachyotis*), diet (*Chrotopterus auritus* and *Centurio senex*), or avoidance of nets and harp traps (*Diphylla ecaudata*, *Molossus rufus*, *Saccopteryx bilineata*) probably explain the rarity of some of the species in our assemblage (Gardner, 1977; Weinbeer and Kalko, 2004).

4.2. Capture methods and inventory completeness

In the Neotropics, the use of complementary methods such as sub-canopy mist nets and harp traps is necessary to determine

Table 3 – Number of individuals, species and proportion of bats assigned into guilds per site

Guilds	Cenote in pastureland			Pastureland			Cenote in forest			Forest		
	S	n	%	S	n	%	S	n	%	S	n	%
Frugivores	6	409	79.2	6	224	78.3	7	946	91.8	8	889	90.2
Aerial insectivores	5	35	6.8	5	14	4.9	5	46	4.4	5	40	4
Gleaning animalivores	4	12	2.3	1	3	1	4	23	2.2	4	22	2.2
Nectarivores	1	19	3.6	1	39	13.7	1	16	1.5	1	30	3
Sanguivores	1	41	8	1	6	2	0	0	0	2	5	0.5

Guilds followed [Simmons and Voss \(1998\)](#).

the habitat use of insectivores or higher-flying species and to maximise inventory completeness ([Kalko and Handley, 2001](#)). Ours is the first study in the region to use such a variety of capture methods. Although we captured most bats in mist nets set at ground level (78% of captures), followed by sub-canopy nets (18%), and caught relatively few bats in harp traps (4%), several species were recorded exclusively in sub-canopy nets or in harp traps, thus justifying our sampling methodology.

The remarkable effectiveness of sub-canopy mist nets set in the pastureland, suspended from isolated trees left by ranchers, confirm the important role of these trees in disturbed areas where they provide food resources, feeding roosts and temporary shelter against possible predators ([Estrada et al., 1993](#); [Galindo-González et al., 2000](#)). Harp traps, designed to capture highly manoeuvrable species such as vespertilionids and emballonurids ([Tuttle, 1974](#)), are up to 60 times more effective than ground mist nets in Old World tropical forest ([Francis, 1989](#)), but appear to be relatively ineffective at sampling many neotropical bats compared to mist nets ([Clarke et al., 2005a,b](#)). Although we captured relatively few bats in the harp trap, two insectivorous species, *Natalus stramineus* and *Micronycteris schmidtorum* were exclusively captured using this method. The Mexican funnel-eared bat, *Natalus stramineus*, has low intensity echolocation calls that are difficult to detect with bat detectors and often avoids mist nets, which explains its absence from many bat inventories ([Rydell et al., 2002](#)). The phyllostomine *Micronycteris schmidtorum* is rarely recorded in the north of Yucatan ([Hernández et al., 1996](#)), and the individual captured in the present study represents only the fifth record of the species in the area.

Although no combination of sampling methods can guarantee complete inventories ([Voss and Emmons, 1996](#)), our results demonstrate that in the Yucatan Peninsula the use of more than one capture method is necessary to record most of the species in the bat assemblage. It is likely however, that additional sampling or the use of methods such as echolocation call analysis could record a few more rare or elusive species, particularly those belonging to the families Molossidae and Emballonuridae that were probably underrepresented in our captures. Molossids have been effectively captured in the region in mist nets set across shallow bodies of water ([Bowles et al., 1990](#); [MacSwiney et al., 2003](#)), but this protocol could not be followed due to the depth of water, up to 100 m, in the cenotes and the presence of crocodiles which were a hazard for the investigators and the trapped bats.

4.3. Importance of forest for bats

Throughout the Yucatan Peninsula, lowland tropical forests have been disturbed both by anthropogenic factors (e.g. Maya culture settlements) and natural phenomena (e.g. hurricanes and wildfires). Our results indicate that the remaining forests in the northern Yucatan Peninsula are extremely important for bats, exhibiting a high species diversity and abundance, and that conversion of forest to pastureland is detrimental to many leaf-nosed bats (Phyllostomidae), evidenced by a lower abundance of frugivores (*Artibeus jamaicensis*, *A. lituratus*, *A. phaeotis* and *Carollia sowelli*) and gleaning animalivores in pastureland. In the neotropics gleaning animalivores are known to be sensitive to forest disturbance ([Fenton et al., 1992](#); [Medellín et al., 2000](#)), and are adversely affected even by low levels of forest disturbance such as selective logging ([Clarke et al., 2005a,b](#)). In this study, only one gleaning animalivore, *Micronycteris microtis*, which seems tolerant of disturbance ([Brosset et al., 1996](#); [Estrada and Coates-Estrada, 2002](#)), was recorded in pastureland without cenotes, areas almost completely deforested with only scattered individual trees.

Our findings are in broad agreement with [Medellín et al. \(2000\)](#) who found a decrease in bat species richness in agricultural landscapes in Chiapas, Mexico, compared to continuous forest, but an increase in abundance of a few species of bats, such as *Sturnira lilium*, which feed on the fruits of pioneer plants ([Medellín et al., 2000](#)). A more extreme case has been documented in Los Tuxtlas, Mexico, where no bats were captured in forested landscapes after their transformation into pastureland. ([Estrada et al., 1993](#)). In contrast to the results obtained by [Estrada et al. \(1993\)](#), we captured 14 species in pastureland despite the potential loss of roosting and foraging sites driven by deforestation. We observed that the key factor for this was the presence of the few trees left by ranchers. Capture rates were significantly greater when nets and harp traps were set around trees in pastureland compared to areas without trees, suggesting that retention of isolated trees in agricultural landscapes has an important role in the conservation of bat assemblages ([Galindo-González et al., 2000](#)).

The remaining forest in the Yucatan is threatened by several factors. In the last few centuries, Yucatan's primary vegetation has been removed for the establishment of crops such as the henequen (sisal, *Agave fourcroydes* Lem.) and citrus ([Flores and Espejel, 1994](#); [González-Iturbe et al., 2002](#)). From the 1970s, conversion of forests into pastures for extensive cattle

ranching has become the leading factor in deforestation (Cairns et al., 1995; González-Iturbe et al., 2002). For example, 60% of Buctzotz county forest, where two of our sampling sites are located, has been converted into pasturelands (INEGI, 2006).

In addition to cattle ranching, the northern Yucatan Peninsula forests are endangered as a result of uncontrolled land development and population expansion due largely to the rapidly expanding tourist industry based around Cancun and along the 'Mayan Riviera'. Future developments should therefore be planned in a manner that is compatible with the conservation of natural forest and in consequence, bat diversity in the region.

4.4. Importance of cenotes for bats

Chrotopterus auritus and *Micronycteris microtis*, both considered threatened in Mexico, and *Eptesicus furinalis*, were exclusively captured at cenotes. *Chrotopterus auritus*, a large carnivorous bat, may be attracted to the frogs and other small vertebrates concentrated around these water bodies in a landscape devoid of pools, streams, and rivers. In pastureland there was a greater species diversity and abundance and number of rare and threatened species at cenotes than sites without cenotes, whereas in forest, sites with and without cenotes had a similar bat assemblage structure, composition and diversity. Within the extensive pastureland of the Yucatan it appears that cenotes are very important for many bats.

We suggest that it may be the vegetation associated with cenotes rather than the water bodies *per se* that attracts many bats in pastureland. In pastureland, cenotes were surrounded by a characteristic dense layer of heterogeneous vegetation, with this mature forest fragment attracting many frugivorous bats and gleaning animalivores, whereas areas of pastureland without cenotes were almost entirely deforested with only scattered individual trees, and harboured far fewer phyllostomids. In contrast, forest had a similar vegetation structure and composition to that found around cenotes, and this is reflected in the similarity in bat species composition and diversity between sites in forest with and without cenotes. The dominant trees that form the tall evergreen forest surrounding cenotes (e.g. *Ficus* spp., *Manilkara zapota*, *Vitex gaumeri*) also occurred in forest without cenotes, and medium to large frugivorous phyllostomids (e.g. *Artibeus jamaicensis*, *A. lituratus* and *A. phaeotis*) which feed on the fruit of these trees (Gardner, 1977), were equally abundant in forest with and without cenotes.

The vegetation associated with cenotes provides roost sites and also food in the form of pollen and fruits for frugivorous bats, and a diverse invertebrate fauna, associated with dense, mature heterogeneous vegetation, for bats that glean insects and small vertebrates. A few species, particularly insectivores, may drink from cenotes, and the small insects above the water are an important source of food. For example, *Myotis keaysi*, was frequently captured at these water bodies. However, despite our use of multiple capture methods, including nets set in the sub-canopy, we caught relatively few aerial insectivores and probably undersampled the emballonurids, molossids, and vesper bats, the bat families likely to include species associated with cenotes. Early detection of

capture devices by aerial insectivores, which almost exclusively rely on echolocation when foraging and commuting and mostly avoid nets, explains the bias against capture of this guild (Berry et al., 2004). Preliminary analysis of echolocation call data suggests aerial insectivores are abundant at cenotes and there is a preference for cenotes as foraging sites by several species which typically avoided our mist nets and harp traps (M.C. MacSwiney, unpublished data).

4.5. Conservation implications

The Mexican list of threatened species has assessed the conservation status of 36 bat species (SEMARNAT, 2002). None of the species recorded in this study have extinction risk status, but five of them are considered threatened: *Lampronnycteris brachyotis*, *Micronycteris schmidtorum*, *Mimon cozumelae*, *Chrotopterus auritus* and *Lonchorhina aurita*. These gleaning animalivores were more abundant in habitats with cenotes and two species, *M. schmidtorum* and *C. auritus*, were exclusively captured at cenotes in pastureland. In contrast, all these threatened bats were absent from pastureland without cenotes, suggesting that in deforested landscapes, such as pastureland, cenotes are particularly important habitats for threatened bats. In such landscapes, cenotes may be thought of as 'oases' of high bat diversity where the conditions created by the presence of water bodies that supports a surrounding plant assembly of tall evergreen trees, appears to attract an abundance of bats of most guilds, including many locally rare and threatened species.

Protected areas have been established in the Yucatan Peninsula for only about 20 years. Originally these areas were created to protect the coastal environments in the north and also forested areas located in the south of the Peninsula, resulting in a lack of connectivity between protected areas. In the past 10 years, local government efforts have focused on establishing new protected areas to create a biological corridor connecting existing ones, particularly in Yucatan, an extremely deforested state at regional and national level (Flores-Villela and Gérez, 1988). Additionally, private protected areas are being established in the north of Quintana Roo, as exemplified by our forested sampling localities. In their search for foraging areas and roosting sites, some highly mobile bat species can traverse open areas (Fleming and Heithaus, 1986; Aguirre et al., 2003). However, the wing morphology and feeding behaviour of forest-dependent bats such as phyllostomines suggests that they are not well adapted to traversing deforested areas for long distances (Kalko et al., 1999). Within this scenario, it is possible that the numerous cenotes and associated vegetation that exist in the agricultural landscape of northern Yucatan Peninsula act as 'stepping stones' facilitating the movement of forest-dependent bats and perhaps other species across deforested areas, between protected areas of forest, thus enhancing biological connectivity.

Unfortunately, there are several potential factors threatening cenotes including water contamination from nitrates as result of untreated domestic and animal waste and nitrogen-rich fertilizer used in agriculture (Pacheco et al., 2001), as well as the removal of the forest surrounding cenotes to facilitate the access of livestock to water (MCM personal

observation). We suggest government efforts should be made to convince local ranchers and other landowners to retain the natural vegetation around cenotes or restore it when it has been removed or degraded. In particular, trees such as *Ficus* spp., *Brosimum alicastrum* and *Manilkara zapota* should be preserved by ranchers to provide shade to livestock enclosures and for forage, as these plants attract an abundance of bats of many species (Estrada et al., 1993). Protection of cenotes in the agricultural landscape and particularly the remaining vegetation surrounding them is vital not only for conserving bats but also because these habitats represent potential seed sources for the regeneration of the deciduous forest of northern Yucatan (González-Iturbe et al., 2002) in which bats play a key role as pollinators and seed dispersers.

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REFERENCES

- Aguirre, L.F., Lens, L., Matthysen, E., 2003. Patterns of roost use by bats in a neotropical savanna: implications for conservation. *Biological Conservation* 111, 435–443.
- Anthony, E.L., 1988. Age determination in bats. In: Kunz, T.H. (Ed.), *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington, DC, pp. 47–59.
- Arita, H.T., 1993. Riqueza de especies de la mastofauna de México. In: Medellín, R.A., Ceballos, G. (Eds.), *Avances en el estudio de los mamíferos de México*. Publicaciones Especiales, Asociación Mexicana de Mastozoología, México, pp. 109–128.
- Arita, H.T., 1997. Species composition and morphological structure of the bat fauna of Yucatan, Mexico. *Journal of Animal Ecology* 66, 83–97.
- Arita, H.T., Vargas, J.A., 1995. Natural history, interspecific association, and incidence of the cave bats of Yucatan, Mexico. *The Southwestern Naturalist* 40, 29–37.
- Audet, D., Engstrom, M., Fenton, M.B., 1993. Morphology, karyology, and echolocation calls of *Rhogeessa* (Chiroptera: Vespertilionidae) from the Yucatan Peninsula. *Journal of Mammalogy* 74, 498–502.
- Barber, A., Tun, J., Crespo, M.B., 2001. A new approach on the bioclimatology and potential vegetation of the Yucatan peninsula (Mexico). *Phytocoenologia* 31, 1–31.
- Berger, W.H., Parker, F.L., 1970. Diversity of planktonic Foraminifera in deep sea sediments. *Science* 168, 1345–1347.
- Berry, N., O'Connor, W., Holderied, M.W., Jones, G., 2004. Detection and avoidance of harp traps by echolocating bats. *Acta Chiropterologica* 6, 335–346.
- Bowles, J.B., Heideman, P.D., Erickson, K.R., 1990. Observations on six species of free-tailed bats (Molossidae) from Yucatan, Mexico. *The Southwestern Naturalist* 35, 151–157.
- Brosset, A., Charles-Dominique, P., Cockle, A., Cosson, J.F., Masson, D., 1996. Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology* 74, 1974–1982.
- Cairns, M.A., Dirzo, R., Zadroga, F., 1995. Forests of Mexico, a diminishing resource? *Journal of Forestry* 93, 21–24.
- Cervantes-Martínez, A., Elías-Gutiérrez, M., Suárez-Morales, E., 2002. Limnological and morphometrical data of eight karstic systems “cenotes” of the Yucatan Peninsula, Mexico, during the dry season (February–May, 2001). *Hydrobiologia* 482, 167–177.
- Chao, A., 1984. Nonparametric-estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11, 265–270.
- Chao, A., Shen, T.J., 2003–2005. Program SPADE (Species Prediction And Diversity Estimation). Program and User's Guide published at <<http://chao.stat.nthu.edu.tw>>.
- Ciechanowski, M., 2002. Community structure and activity of bats (Chiroptera) over different water bodies. *Mammalian Biology* 67, 276–285.
- Clarke, F.M., Pio, D.V., Racey, P.A., 2005a. A comparison of logging systems and bat diversity in the Neotropics. *Conservation Biology* 19, 1194–1204.
- Clarke, F.M., Rostant, L.V., Racey, P.A., 2005b. Life after logging: post-logging recovery of a neotropical bat community. *Journal of Applied Ecology* 42, 409–420.
- Cosson, J.F., Pons, J.M., Masson, D., 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology* 15, 515–534.
- Dytham, C., 2005. *Choosing and Using Statistics: A Biologist's Guide*, second ed. Blackwell Publishing, United Kingdom.
- Elangovan, V., Marimuthu, G., 2001. Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. *Journal of Zoology* 253, 347–350.
- Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biological Conservation* 103, 237–245.
- Estrada, A., Coates-Estrada, R., Meritt Jr., D., 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* 16, 309–318.
- Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B., Merriman, C., Obrist, M.K., Syme, S.M., 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* 24, 440–446.
- Fenton, M.B., Bernard, E., Bouchard, S., Hollis, L., Johnston, D.S., Lausen, C.L., Ratcliffe, J.M., Riskin, D.K., Taylor, J.R., Zigouris, J., 2001. The bat fauna of Lamanai, Belize: roosts and trophic roles. *Journal of Tropical Ecology* 17, 511–524.
- Findley, J.S., 1993. *Bats: A Community Perspective*. Cambridge University Press, Cambridge.
- Fleming, T.H., Heithaus, E.R., 1986. Seasonal foraging behavior of the frugivorous bat *Carollia perspicillata*. *Journal of Mammalogy* 67, 660–671.
- Flores, J.S., Espejel, I., 1994. Tipos de vegetación de la Península de Yucatán. *Etnoflora Yucatanense*. Universidad Autónoma de Yucatán, México.
- Flores-Villela, O., Gérez, P., 1988. Conservación en México: síntesis sobre vertebrados terrestres, vegetación y uso del suelo. Instituto Nacional de Investigaciones sobre Recursos Bióticos, Conservación Internacional, México.
- Francis, C.M., 1989. A comparison of mist nets and two designs of harp traps for capturing bats. *Journal of Mammalogy* 70, 865–870.
- Galindo-González, J., Guevara, S., Sosa, V.J., 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology* 14, 1693–1703.
- Gardner, A.L., 1977. Feeding habits. In: Baker, R.J., Jones, J., Jr., Carter, D.C. (Eds.), *Biology of Bats of the New World Family*

- Phyllostomidae. Part II. Special Publications. Texas Technical University, Lubbock, pp. 293–350.
- Gómez-Pompa, A., 2003. Research challenges for the lowland Maya area: an introduction. In: Gómez-Pompa, A., Allen, M.F., Fedick, S.L., Jiménez-Osornio, J.J. (Eds.), *The Lowland Maya Area. Three Millennia at the Human–Wildland Interface*. The Haworth Press, pp. 3–9.
- González-Iturbe, J.A., Olmsted, I., Tun-Dzul, F., 2002. Tropical dry forest recovery after long term henequen (sisal, *Agave fourcroydes* lem.) plantation in northern Yucatan, Mexico. *Forest Ecology and Management* 167, 67–82.
- Greenhall, A.M., Joermann, G., Schmidt, U., 1983. *Desmodus rotundus*. *Mammalian Species* 202, 1–6.
- Handley Jr., C.O., Wilson, D.E., Gardner, A.L., 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, in Barro Colorado Island, Panama. In: *Smithsonian Contributions to Zoology*. Smithsonian Institution Press, Washington, DC.
- Heithaus, E.R., Fleming, T.H., Opler, P.A., 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56, 841–854.
- Hernández, S., Sánchez-Cordero, V., Sosa-Escalante, J., Segovia, A., 1996. Lista anotada de los mamíferos terrestres de la Reserva de Dzilam, Yucatán, México. *Listados Faunísticos de México*. Instituto de Biología, Universidad Nacional Autónoma de México.
- INEGI (Instituto Nacional de Estadística, Geografía e Informática), 2006. Anuario estadístico. Yucatán. Gobierno del Estado de Yucatán. INEGI (Instituto Nacional de Estadística, Geografía e Informática), México.
- Jones Jr., K., Smith, J., Genoways, H., 1973. Annotated checklist of mammals of the Yucatan Peninsula, Mexico. I. Chiroptera. *Occasional Papers of the Museum of Texas Tech University* 13, 1–31.
- Kalko, E.K.V., Handley, C.O., 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology* 153, 319–333.
- Kalko, E.K.V., Handley Jr., C.O., Handley, D., 1996. Organization, diversity and long-term dynamics of a neotropical bat community. In: Cody, M., Smallwood, J. (Eds.), *Long-term Studies of Vertebrate Communities*. Academic Press, Los Angeles, CA, pp. 503–553.
- Kalko, E.K.V., Friemel, D., Handley Jr., C.O., Schnitzler, H.-U., 1999. Roosting and foraging behaviour of two neotropical gleaner bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* 31, 344–353.
- Kunz, T.H., Kurta, A., 1988. Capture methods and holding devices. In: Kunz, T.H. (Ed.), *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington, DC, pp. 1–29.
- Lemke, T.O., 1984. Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. *Ecology* 65, 538–548.
- MacSwiney G., M.C., 2000. Estructura de la comunidad de quirópteros de la Reserva Ecológica de “El Edén”, Quintana Roo, México. BSc thesis. Facultad de Medicina Veterinaria y Zootecnia. Universidad Autónoma de Yucatán, México.
- MacSwiney G., M.C., Sosa-Escalante, J., Sélem-Salas, C.I., 2003. Ampliación en la distribución de *Eumops underwoodi* Goodwin 1940 (Chiroptera Molossidae) en la Península de Yucatán, México. *Revista Mexicana de Mastozoología* 7, 55–57.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing, United Kingdom.
- Medellín, R.A., 1993. Estructura y diversidad de una comunidad de murciélagos en el trópico húmedo mexicano. In: Medellín, R.A., Ceballos, G. (Eds.), *Avances en el Estudio de los Mamíferos de México*. Publicaciones Especiales, Asociación Mexicana de Mastozoología, México, pp. 333–350.
- Medellín, R.A., Gaona, O., 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica* 31, 478–485.
- Medellín, R.A., Arita, H.T., Sánchez, H., O., 1997. Identificación de los murciélagos de México. Clave de campo. Publicaciones Especiales, Asociación Mexicana de Mastozoología, México.
- Medellín, R.A., Equihua, M., Amín, M.A., 2000. Bat diversity and abundance as indicators of disturbance in neotropical Rainforests. *Conservation Biology* 14, 1666–1675.
- Morrison, D.W., 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera Phyllostomidae). *Animal Behaviour* 26, 852–855.
- Munn, C.A., 1991. Tropical canopy netting and shooting lines over tall trees. *Journal of Field Ornithology* 62, 454–463.
- Pacheco, J., Marín, L., Cabrera, A., Steinich, B., Escolero, O., 2001. Nitrate temporal and spatial patterns in 12 water-supply wells, Yucatan, Mexico. *Environmental Geology* 40, 708–715.
- Racey, P.A., 1988. Reproductive assessment in bats. In: Kunz, T.H. (Ed.), *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington, DC, pp. 31–45.
- Reid, F., 1997. *A Field Guide to the Mammals of Central America and Southeast Mexico*. Oxford University Press.
- Rodríguez-Durán, A., Vázquez, R., 2001. The bat *Artibeus jamaicensis* in Puerto Rico (West Indies): seasonality of diet, activity, and effect of a hurricane. *Acta Chiropterologica* 3, 53–61.
- Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in Northern Ireland: implications for conservation. *Biological Conservation* 108, 49–58.
- Rydell, J., Miller, L.A., Jensen, M.E., 1999. Echolocation constraints of Daubenton's bat foraging over water. *Functional Ecology* 13, 247–255.
- Rydell, J., Arita, H.T., Santos, M., Granados, J., 2002. Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *Journal of Zoology* 257, 27–36.
- Schmitter-Soto, J.J., Comin, E.A., Escobar-Briones, E., Herrera-Silveira, J., Alcocer, J., Suarez-Morales, E., Elias-Gutiérrez, M., Diaz-Arce, V., Marín, L.E., Steinich, B., 2002. Hydrogeochemical and biological characteristics of cenotes in the Yucatan Peninsula (SE Mexico). *Hydrobiologia* 467, 215–228.
- Schultz, G.P., 2003. Structure and diversity of the forests at the El Edén Ecological Reserve. In: Gómez-Pompa, A., Allen, M.F., Fedick, S.L., Jiménez-Osornio, J.J. (Eds.), *The Lowland Maya Area. Three Millennia at the Human–Wildland Interface*. The Haworth Press, pp. 91–114.
- Schultz, G.P., 2005. Vascular flora of the El Edén Ecological Reserve, Quintana Roo, Mexico. *Journal of the Torrey Botanical Society* 132, 311–322.
- Schulze, M.D., Seavy, N.E., Whitacre, D.F., 2000. A comparison of the phyllostomid bat assemblages in undisturbed neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Petén, Guatemala. *Biotropica* 32, 174–184.
- SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales), 2002. Norma Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental-Especies nativas de México de flora y fauna silvestres- Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. second ed. Diario Oficial. 06 March 2002, pp. 1–56.
- Simmons, N.B., 2005. Order Chiroptera. In: Wilson, D.E., Reeder, D.M. (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference*, third ed. Johns Hopkins University Press, pp. 312–529.
- Simmons, N.B., Voss, R.S., 1998. The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna. I. Bats. *Bulletin of the American Museum of Natural History* 237, 1–129.
- Simpson, E.H., 1949. Measurement of diversity. *Nature* 163, 688.

- Solow, A.R., 1993. A simple test for change in community structure. *Journal of Animal Ecology* 62, 191–193.
- Sosa-Escalante, J., 1997. Ecología de la comunidad de mamíferos terrestres del noreste de la Península de Yucatán, México: diversidad, distribución y estructura. MSc thesis. Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Tuttle, M.D., 1974. Improved trap for bats. *Journal of Mammalogy* 55, 475–477.
- Voss, R.S., Emmons, L.H., 1996. Mammalian diversity in neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* 230, 1–115.
- Weinbeer, M., Kalko, E.K.V., 2004. Morphological characteristics predict alternate foraging strategy and microhabitat selection in the orange-bellied bat, *Lamproncycteris brachyotis*. *Journal of Mammalogy* 85, 1116–1123.